From passive to informed: mechanical mechanisms of seed dispersal

Title

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Summary

Plant dispersal mechanisms rely on anatomical and morphological adaptations for the use of physical or biological dispersal vectors. Recently, studies of interactions between the dispersal unit and physical environment have uncovered fluid dynamic mechanisms of seed flight, protective measures against fire, and release mechanisms of explosive dispersers. Although environmental conditions generally dictate dispersal distances, plants are not purely passive players in these processes. Evidence suggests that some plants may enact informed dispersal, where dispersal-related traits are modified according to the environment. This can occur via developmental regulation, but also on shorter timescales via structural remodelling in relation to water availability and temperature. Linking interactions between dispersal mechanisms and environmental conditions will be essential to fully understand population dynamics and distributions.

Keywords

Dispersal, informed dispersal, biomechanics, diaspore, seed, bet-hedging

Introduction

From everyday occurrences, such as the flight of a dandelion fruit or animals consuming seeds, to the extreme events of seed release after burning or explosive ejection – dispersal is a physical process in which seeds or fruits are moved from one location to another. As a result, plants have evolved dispersal units (diaspores) with diverse and often complex structures to facilitate movement either by self-derived energy sources (e.g. explosive dispersal) or via environmental or biotic carriers. Construction of the seeds and all the specialised coverings and appendages around them is an energy expensive process. While seed dispersal may appear to be under limited biological control, an emerging picture suggests that plants have evolved various strategies to increase their fitness through selective dispersal.

Mechanical mechanisms of dispersal

Flight mechanisms

Wind dispersal is common given the ubiquitous presence of wind in virtually all environments. Appendages enabling flight are not absolutely required as even non-specialised seeds may be wind dispersed, but the presence of membranous wings or fluffy hairs substantially enhances dispersal potential (Tackenberg *et al.*, 2003).

Winged maple seeds autorotate and generate lift as they fall by adopting a highly optimised shape, size and angle of attack to form a leading edge vortex (Fig. 1a) (Lentink *et al.*, 2009). Compared to simple gliding such as in birch tree seeds, the maple vortex and corresponding autorotation bestow a greater descent time for a given size and weight (Lentink *et al.*, 2009). In contrast to the single-bladed maple seeds, Dipterocarpaceae adopt a multiple-winged approach to autorotating flight (Fig. 1b). Similarly to maples, the square root of wing loading (weight divided by wing area) is a good predictor of the falling velocity. However, this cannot fully explain the observed relationship between weight and falling velocity of 3D printed seed models with differing wing curvature (Rabault *et al.*, 2019; Fauli *et al.*, 2019). Instead, it appears that fruits adopt an optimum wing curvature to maximise descent time. This morphology incorporates a curvature and length that ensures a significant proportion of the wing tip is oriented almost horizontally. Spinning of the fruit occurs by a helicopter-like mechanism in which the horizontal force on the wings promotes greater forward lift than reverse drag (Rabault *et al.*, 2019; Fauli *et al.*, 2019).

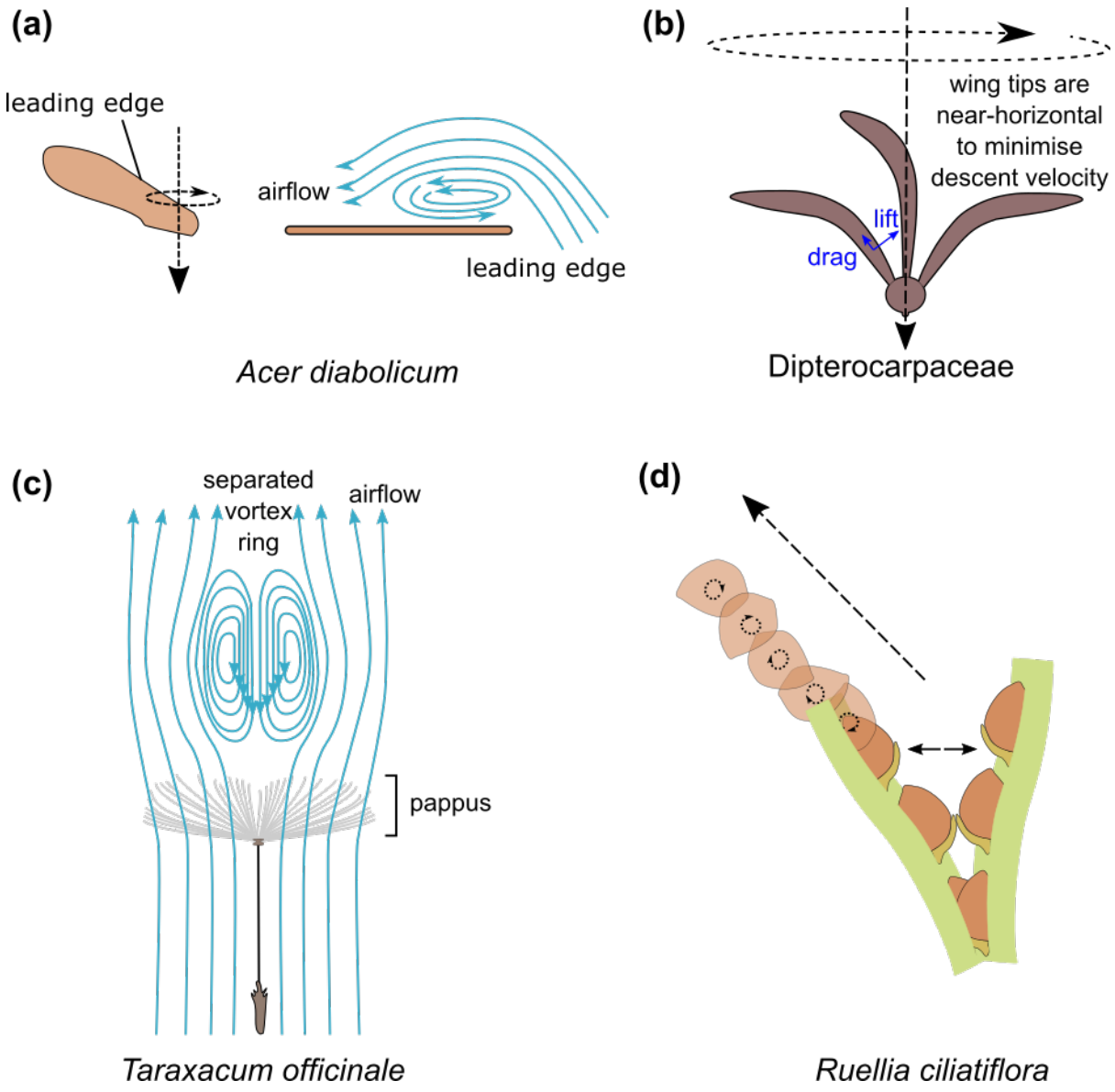

Figure 1. Mechanical mechanisms of dispersal. **(a)** schematic of a maple samara illustrating the direction of autorotation and descent and the airflow around a cross section of the samara forming a leading edge vortex, **(b)** schematic of a typical Dipterocarp diaspore illustrating the rotating motion and direction of descent during flight with blue arrows representing lift and drag forces acting on a wing segment, **(c)** schematic of a dandelion diaspore illustrating the streamlines of airflow through and around the pappus, **(d)** schematic of *Ruellia ciliatiflora* explosive seed ejection demonstrating backspin induced by the launch orientation.

For smaller or lighter diaspores, wings are not necessary for efficient flight. Hairs or bristles form the pappus of many Asteraceae diaspores, and similar structures have independently evolved in other families, such as the Apocynaceae. The dandelion pappus bears around 100 fine hairs made of hollow dead cells (Cummins *et al.*, 2018). These hairs occupy only around 10% of the pappus structure, with empty space between them and this spacing is crucial to the flight mechanism. Visualisation of the flow in the wake of the pappus has

uncovered a separated vortex ring in which air stably recirculates at a short distance from the pappus itself (Cummins *et al.*, 2018) (Fig. 1c). This is due to a boundary layer of relatively viscous air, which cannot easily pass between the hairs. Instead, the majority of flow is forced around the outer edges of the pappus. At the speed that the dandelion diaspore typically falls through the air, reduced porosity (more closely spaced hairs) would cause the vortex to shed asymmetrically from the pappus, destabilising its flight. Conversely, increased porosity or fewer hairs would allow air to easily pass between them and drag force would be reduced (Cummins *et al.*, 2018).

Animal dispersal

In addition to facilitating flight, the hairs of the dandelion pappus bear microscopic barbs that could facilitate secondary dispersal by sticking to animals (Meng *et al.*, 2014) and hooks on their fruits that increase friction with the soil (Grohmann *et al.*, 2019) potentially allowing them to remain within the soil in a particular location. Indeed, a common alternative to wind dispersal is to stick to animal coats or soil particles via hooks (Gorb & Gorb, 2002; Chen *et al.*, 2013; Horbens *et al.*, 2015) or glue (Western, 2012; Kreitschitz *et al.*, 2015; Lenser *et al.*, 2016; Arshad *et al.*, 2019). In Martyniaceae fruit, a curved structure with transverse fibres allows bending behaviour while hooking, and longitudinally arranged sclerenchyma appear to enhance tensile strength (Horbens *et al.*, 2015).

Explosive dispersal

Explosive seed dispersal is also heavily reliant on mechanical phenomena. Elastic energy is stored in fruit tissue during deformation induced by dehydration, for example Geraniaceae fruits (Abraham & Elbaum, 2013), or in some cases, by excessive hydration building up turgor pressure, for example in *Impatiens capensis* (Hayashi *et al.*, 2009). In *Cardamine hirsuta*, a bilayer structure leads to differential contraction and expansion in response to hydrostatic pressure according to polarised lignification patterns (Hofhuis *et al.*, 2016).

During explosive pod shatter, it is not only the magnitude of force that is important but also the manner in which seeds are launched. For *Ruellia ciliatiflora* seeds (Fig. 1d), those released from more distal parts of the fruit are suddenly pulled sideways by the bending of the fruit septa (Cooper *et al.*, 2018). This results in horizontal motion of the curved retinacula that cradle and orientate the round, flattened seeds. This careful orientation during launch produces a backspin on many of the seeds that causes them to spin like a frisbee. The spinning motion gyroscopically stabilises their flight leading to reduced drag forces on the seeds and increased dispersal distances compared to seeds that do not spin (Cooper *et al.*, 2018).

Informed dispersal: controlled dispersal in response to the environment

Intricate dispersal structures and mechanisms have clearly evolved in response to selective pressures to make use of specific physical or biotic vectors. Beyond heritable adaptation, however, it often appears that plants are quite passive players in dispersal, relying on the weather or animals to come along at just the right moment.

This can be contrasted to animal migration and dispersal in which individuals can acquire information about their environment to make decisions about their movements in a process named informed dispersal. Acquisition of environmental information and subsequent modification of development or behaviour can take place both before dispersal, during translocation and at the stage of settlement (Clobert *et al.*, 2009). For example, exploratory behaviour of red squirrels is more extensive in individuals originating from poorer quality habitats (Haughland & Larsen, 2004). *Erigone atra* spiders modify their dispersal either by

forming bridging threads to move to neighbouring plants or by forming a sail-like structure out of their silk for longer distance dispersal. The prevalence of these behaviours is influenced by the temperature they experience when young (Bonte *et al.*, 2008). In this vein, the concept of informed dispersal has been applied largely to animal dispersal only; there

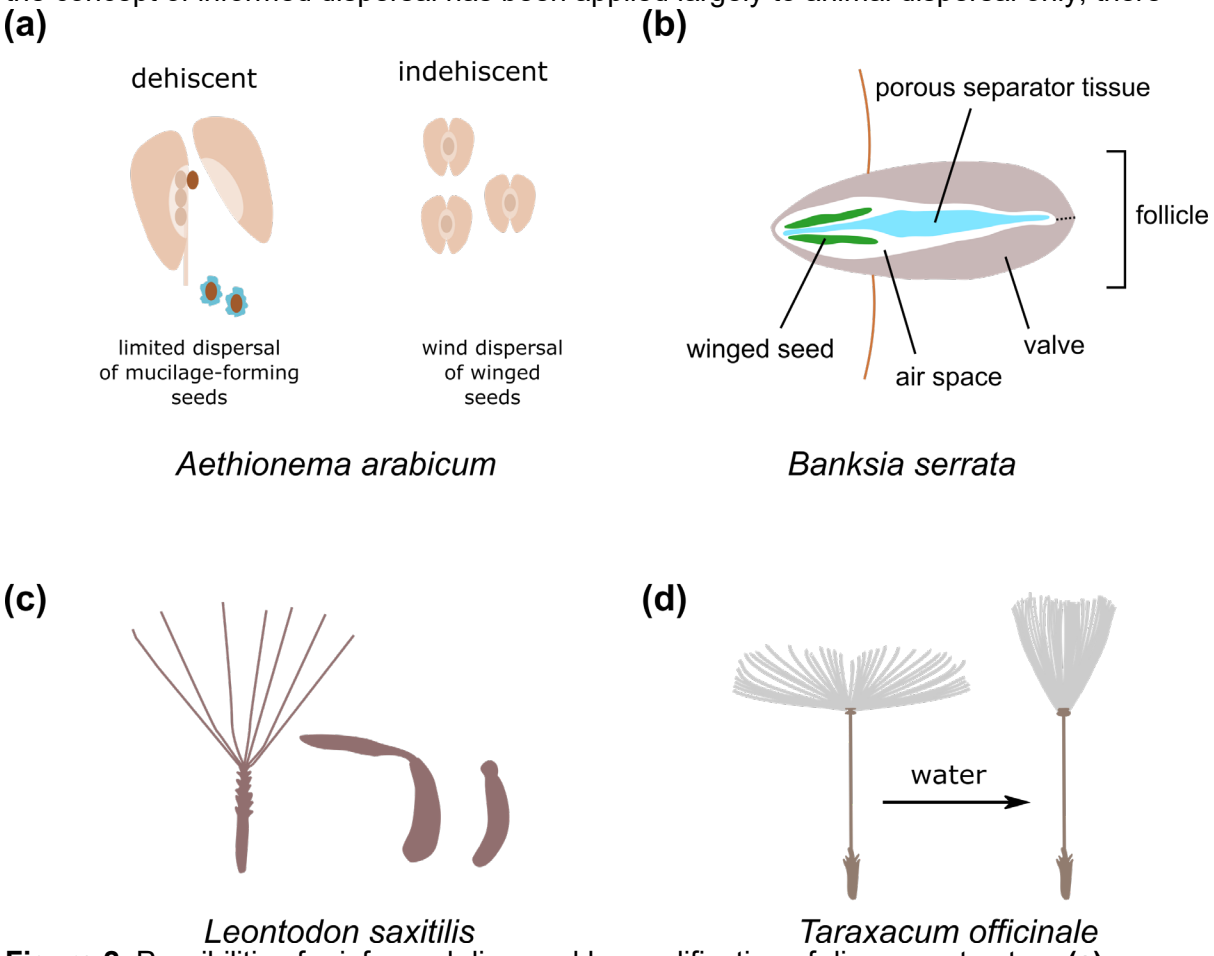

Figure 2. Possibilities for informed dispersal by modification of diaspore structure **(a)** schematic of *Aethionema arabicum* fruits indicating fruit heteromorphism leading to differential dispersal of seeds, **(b)** longitudinal schematic of *Banksia serrata* morphology demonstrating valves that open during fire exposure, **(c)** schematic of *Leontodon saxitilis* diaspores highlighting heteromorphism in fruit structure, **(d)** schematic demonstrating dandelion pappus closure on exposure to water.

are clear cases, however, in which plants exert control over dispersal by altering their development or responding to environmental conditions.

Long-term responses via developmental plasticity

In plants, evidence for informed dispersal is so far limited to cases where environmental information is acquired before dispersal begins. Environmental responses occur in relation to the initiation of dispersal rather than translocation and are largely mediated by developmental plasticity of seed or fruit morphology. There are numerous examples in which different seed or fruit morphs are produced on the same plant (Fig. 2a,c), particularly in the Asteraceae but also in at least 17 other plant families (Imbert, 2002). Diaspores may vary in weight or size or may possess different dispersal appendages, such as the presence or absence of a pappus or wing (Imbert, 2002). Diaspore heteromorphism can be a predetermined bet-hedging strategy but can also be environmentally responsive indicating

that informed dispersal may occur. *Crepis sancta*, for example, produces a greater proportion of pappus-bearing fruits when nutrients are depleted, suggesting there may be increased average dispersal distances (Imbert & Ronce, 2001).

The Brassica, *Aethionema arabicum*, forms dehiscent fruits that open to release seeds directly into the nearby proximity, as well as indehiscent winged fruits that carry seeds further by wind (Fig. 2a) (Lenser *et al.*, 2016; Arshad *et al.*, 2019). One possibility, is that at lower temperatures, which may signify a higher altitude and a harsher, less predictable environment, a greater proportion of the winged indehiscent fruits are produced that may disperse further (Lenser *et al.*, 2016; Arshad *et al.*, 2019). This bet-hedging strategy is further enhanced by the production of mucilage by the seeds of dehiscent fruits but not those of indehiscent fruits. Arshad *et al.*, (2019) demonstrate that this causes the less-dispersed seeds to stick more easily to wet sand and remain in their immediate environment.

Martorell & Martínez-López (2014) demonstrated informed dispersal in field conditions by planting heterocarpic *Heterosperma pinnatum* at varying planting densities and soil moisture availabilities. They found a greater proportion of dispersible (awned) diaspores formed in adverse conditions where competition was greater, particularly when soil moisture was low. Awned diaspores may therefore enable greater dispersal potential to escape a poor quality local environment. The change in ratio of diaspore types in these examples gives a strong indication that informed dispersal is occurring, but measuring actual dispersal distances and seedling establishment in these conditions would be informative to establish whether the perceived benefits of this developmental plasticity are actually realised.

In some cases, not only do different diaspore morphs exhibit differential dispersal capacity, but also differential germination abilities and fitness in specific environmental conditions (Gardocki *et al.*, 2000; Brändel, 2007). This suggests that dispersal and germination strategies are co-ordinated make best use of specific microclimates.

Developmental plasticity of diaspore morphology provides an important mechanism for plants to control dispersal distances and influence germination locations. Given the timescales involved in developing seeds and fruits, it is likely that environmental conditions informing developmental plasticity are sensed and responded to over periods of at least days, if not weeks, months or seasons. As a result, developmental plasticity of diaspores is a relatively long-term response, useful for responding to predictable, stable conditions.

Short-term responses via environmentally sensitive morphing

In comparison to long-term responses, the question naturally arises of whether plants are capable of adjusting dispersal in response to more transient conditions. There is some evidence that mechanical features of some plant structures can interact with the local environment during dispersal. For example, abscission bias occurs in many wind-dispersed species (e.g. Asteraceae such as *Cirsium arvense* and in maple - *Acer saccharinum* - samaras). This is where there is a threshold level of wind force required to detach the diaspore from the parent plant and initiate dispersal (e.g. Greene & Johnson, 1992; Jongejans *et al.*, 2007; Treep *et al.*, 2018). The threshold, imposed by the strength of the attachment site, biases dispersal in favour of transient gusts of wind. These are likely to be faster and more turbulent than background wind levels, leading to enhanced dispersal distances (Greene, 2005; Schippers & Jongejans, 2005; Soons & Bullock, 2008; Maurer *et al.*, 2013; Thompson & Katul, 2013).

Abscission bias, though effective on short timescales, is not inherently a form of informed dispersal as it is a passive strategy, rather than a specific response to a varying environment. In some cases, however, detachment force thresholds are not fixed, but can

alter in response to local, often transient, environmental conditions. For example, pine cone scales reversibly close when wet, preventing the detachment of the winged diaspores (Dawson *et al.*, 1997). Additionally, moisture causes the pappus of many Asteraceae species to morph into a different shape where the hairs are brought together, closing the pappus (Fig. 2d) (Taliev, 1894 as cited in Rothert, 1895). For dandelions, this alters aerodynamic flow around the diaspores, which exhibit reduced drag and smaller separated vortex rings (Seale *et al.*, 2019). Closing the pappus in response to moisture reduces their capacity to detach from the parent plant in response to air flow (Seale *et al.*, 2019). This may retain seeds in moist environments beneficial for germination or may promote dispersal in dry conditions more suitable for flight. Water availability is clearly an important regulator of dispersal though with different manifestations, for example moisture triggers dispersal in many desert plants (Gutterman, 2002). Additionally, for maples and Asteraceae plants, water appears to control the start point of dispersal, while the endpoint is controlled for *Aethionema arabicum* seeds that produce mucilage to stick to wet sand (Arshad *et al.*, 2019).

The fire-triggered dispersal of *Banksia* seeds can be considered an informed strategy to find a favourable habitat with less competition. The valves of the seed pods (follicles) are triggered to open during heating, exposing the wing-bearing seeds to air flow (Fig. 2b) (Huss *et al.*, 2018). The thick covering of maternal tissues comprising the valve can insulate the delicate seeds from temperatures of up to 450°C during fire (Huss *et al.*, 2019). The cone rachis combined with thick valves of the follicles and a porous plug-like structure that separates seeds within the follicle are all protective. These structures, combined with a thin air layer, insulate the internal regions, so for the seeds located deep within the follicles, temperature is limited to no more than 100°C during fire exposure. The highly curved valves maintain a high flexural rigidity, but during heating, the lignin in the valves may soften allowing the valves to relax and separate to open the follicle (Huss *et al.*, 2018).

These short-term dispersal responses may be particularly important in unpredictable environments or to respond to conditions that are inherently unpredictable, such as wind gusts and precipitation. The intimate link between moisture and dispersal may not be surprising, given that water is often the activator of seed germination. It may also arise because plant tissue morphing tends to be actuated via differential hydration of the cells (turgor) and the structural materials (e.g. cell wall) (Dumais & Forterre, 2011). Beyond moisture, other types of short-term environmental responses to control dispersal are beginning to emerge. For example, Brassicaceae species actively regulate silique dehiscence in response to temperature (Li *et al.*, 2018). This brings about several questions – are there forms of informed dispersal where other factors affect plant fitness, such as light and essential nutrients? Is there genetic variation within species for these adaptive informed dispersal processes? Future research may uncover the diversity and extent to which these mechanisms occur.

Conclusions

Dispersal is the only way that plants can move from one location to another so it is not surprising that plants have adopted many physical mechanisms to achieve this. By modifying precisely tuned anatomy and morphology, many plants can exert some control over their dispersal. This arises from interactions between the plant's structure and environmental factors, including those that enable dispersal itself (such as wind), but also factors more important for subsequent plant growth and survival, such as temperature and moisture.

There is currently little mechanistic understanding of the physical ways in which dispersal processes are controlled and tuned by environmental conditions; ecological models of species distributions tend to incorporate only heavily simplified measures of dispersal characteristics. As climate change alters environmental conditions, it will become increasingly necessary to understand and embed these dispersal-environment interactions into models in order to predict their ecological consequences.

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